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Fossil Calidridinae (Aves: Charadriiformes) from the Middle Miocene of the Nördlinger Ries

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Abstract: A new genus of sandpiper, *Mirolia*, is described from middle Miocene lake deposits in southern Germany. It comprises four new species, one of them placed tentatively in the genus. The close relationship to recent genera *Philomachus* and *Tryngites* on one side and the occurrence of the fossil Calidridinae together with tropical birds, like *Capitonidae*, on the other side make it likely that the fossil sandpipers were migrating birds. A contribution to the osteology of the Scolopacidae, especially the Calidridinae, is given.

Key words: *Mirolia*, gen. nov.; *Mirolia brevirostrata* spec. nov., *Mirolia dubia* spec. nov., *Mirolia parvula* spec. nov., *Mirolia? mascalidris* spec. nov., Nördlinger Ries, Miocene, Germany.

1. THE NÖRDLINGER RIES

The Ries is a remarkable basin situated in southern Germany to the north of the Danube, roughly at the centre of a triangle formed by the cities of Stuttgart, Nürnberg and Munich. It is an ancient crater formed by the impact of a meteorite. The event has been dated at 14.8 ± 0.7 Ma.

During the middle Miocene period subsequent to the impact, the Ries was a lake without an outlet. The sediments deposited in the deeper parts of the lake are layered clays and marls, whereas in the shoal facies a massive calcareous sinter was formed by algal bioherms, especially in freshwater environments at the mouth of creeks or brooks.

At present, the Ries is a roughly circular depression of over 20 km in diameter and a depth of 100 – 150 m. The calcareous sinter sticks out in the form of travertine hills over the clays and marls. Several of these hills have yielded a rich and well preserved fossil vertebrate fauna consisting in the first place of birds and mammals.

Fossil birds from the Ries are known since the late 19th century, when more than ten species, mainly large and medium-sized waterbirds such as *Pelecanidae*, *Phalacrocoracidae*, *Anatidae* and *Palaelodidae* were described (LAMBRECHT 1933: 677).

New finds include inland water birds of small size such as *Rallidae*, *Charadriidae*, *Scolopacidae* and *Glareolidae*, as well as landbirds such as *Strigiformes*, small *Phasianidae*, *Psittacidae*, *Coliidae*, *Apodidae*, *Capitonidae* and a great number of *Passeriformes*.

Of this new material only the *Glareolidae* and the *Capitonidae* (BALLMANN 1979, 1983) have yet been de-

scribed. Breeding of the pratincole *Mioglareola gregaria* at the Ries lake was proven by the find of an os medullare. Together with the occurrence of the barbet *Capitonides protractus*, closely related to recent *Trachyphonus*, this breeding record allowed conclusions regarding the environment. The climate of the Nördlinger Ries in the middle Miocene was characterized by warm, dry summers and mild winters, similar to the recent Csa-Climate in the classification by KÖPPEN (1936). The development of the supraorbital gland in *Mioglareola* indicates that the lake had a tendency to salinity. This conclusion is supported by sedimentological data (WOLFF & FÜCHTBAUER 1976).

The remains of mammals represent almost exclusively small rodents, lagomorpha, insectivora and bats. Most of the bones were probably regurgitated by birds of prey, mainly owls, into fissures and holes. A preliminary list of 22 species of mammals is given by HEIZMANN & FAHLBUSCH (1983). They determined the age of this fauna as lower Astaracian, which corresponds to the Neogene Mammal Unit MN 6.

A more recent list of the fossil birds described from the Nördlinger Ries was published by HEIZMANN & HESSE (1995).

2. MATERIAL AND METHODS

The fossil material on which the present paper is based, consists of 127 single skeleton elements, most of them postcranial, but also including skull and mandibula. The state of preservation is excellent, many of the postcranial elements are entire.

Most of the fossils were found at the locality of Steinberg near Deiningen, a few at the locality of Goldberg near Nördlingen.

Skeletons of all the recent species mentioned in this paper have been available for comparison purposes.

The methods are the same as in the previous papers of the author. For details, especially definitions of linear measurements between osteometric points, see BALLMANN (1979). Anatomical terminology has been adopted from the *Nomina Anatomica Avium* (BAUMEL et al. 1993).

The holotypes and most of the material are kept in the Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich under the numbers 1970 XVIII STEINBERG and 1966 XXXIV GOLDBERG. Some specimens are from the Naturhistorisches Museum Basel and a few from the private collection of Dr. E. HEIZMANN.

3. TAXONOMIC SETTING

The Charadriiformes are suited more than most other groups for systematics based on osteological characters. On one side they show a great morphological variety, comprising well differentiated families such as Alcidae, Glareolidae, Pedionomidae, Scolopacidae etc. On the other side the bulk of the order definitely is a natural assemblage characterized by unique osteological features, like the canalis n. coracobrachialis cranialis or the diagnostic shape of the processus supracondylaris dorsalis, both on the humerus.

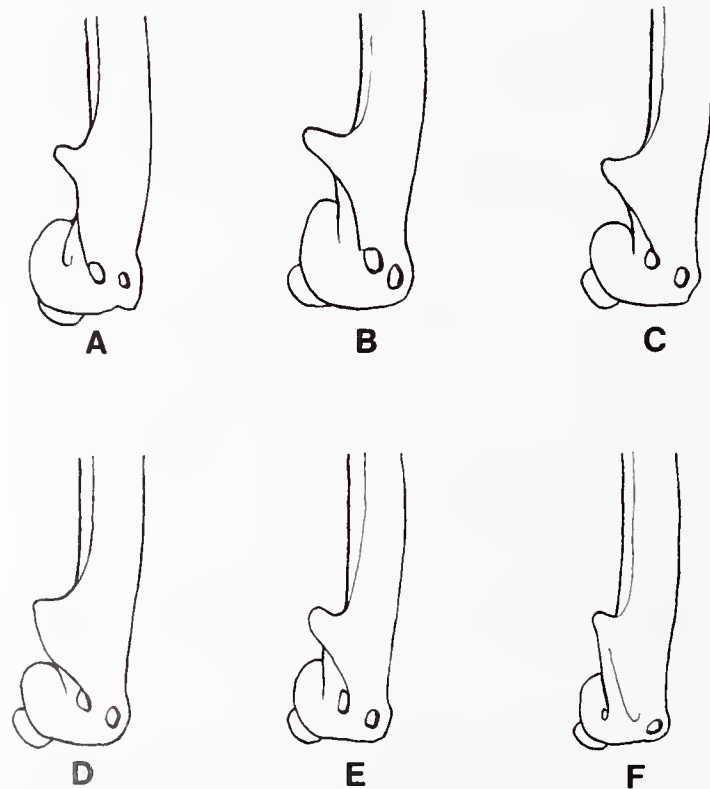


Fig 1: Humeri of Charadriiformes with processus supracondylaris dorsalis in dorsal view, not to scale. A= *Gallinago*, B= *Glareola*, C= *Philomachus*, D= *Limicola*, E= *Tringa*, F= *Charadrius*.

As an example of one of these characteristic features, the processus supracondylaris dorsalis on the humerus is shown on Fig. 1. Its shape can also help to further subdivide the Charadriiformes.

There are, of course, a few marginal or even controversial forms such as *Burhinus* or *Pluvianus*, where this character is feebly expressed or even missing, but they are a small minority compared to the great number of species, which are unquestionably charadriiform.

Accordingly, an attempt has been made to derive a classification of Charadriiformes from osteology (STRAUCH 1978). His paper was based on 227 species, 70 different osteological characters and applied modern techniques like data processing and character compatibility analysis. STRAUCH has not only the merit of presenting a wealth of data in a systematic and transparent way, but also of arriving at some conclusions which were convincing and had not been stressed sufficiently before, like the clear separation of the Charadriidae from the Scolopacidae.

However, a few shortcomings should be noted as well:

- Some important characters have been overlooked, such as the canalis n. coracobrachialis cranialis on the humerus, a unique feature found only in Charadriiformes.

- STRAUCH's osteological terminology is rather vague, which leads to confusions in some of the complex parts of the postcranial skeleton, like the proximal humerus. Also, in the hypotarsus some tendons have not correctly been attributed to their tendinal canals. Of the six assumed homologies two appear to be wrong.

Again, on tab. 1, p. 286, the whole *Charadrius-Vanellus* group has been coded as B for character 64, which would mean that the tendon of m. flexor digitorum longus is located in an osseus canal. It runs in a groove instead and should therefore be coded as A.

This list of minor imperfections should not be continued here, because they might not invalidate any of STRAUCH's conclusions. But there remains one major problem: his coding of the osteological characters is sometimes based on the criterium whether a character is derived or primitive. This decision, however, cannot always be made beforehand and it is because of this, his conclusions might not always be correct. In the case of *Burhinus*, which has vexed whole generations of morphologists, STRAUCH assumes that the aberrant features are derived. The fossil record would rather support the opposite view (OLSON 1985).

In spite of this, the general aspect of STRAUCH's phylogenetic tree of the Charadriiformes compares favourably with the attempts by other authors. The left branch of STRAUCH's final estimate of the phylogeny of the

order is therefore taken as a reference system for the systematics in the present paper. The calidridine and tringine taxa (see Tables 1 and 2) to which the fossils from the Ries under consideration show close resemblance are, with one exception, located in node 9 of his phylogenetic tree (STRAUCH 1978, fig. 36).

BJÖRKLUND (1994) reanalyzed the data presented by STRAUCH applying cladistic methods. His conclusions are mainly limited to the higher taxonomic levels. Another, more detailed reanalysis, also applying cladistics, was carried out by CHU (1997). He discussed

and recoded several of STRAUCH's characters. As far as his conclusions concern the present study, he agrees with STRAUCH in making a clear distinction between plover-like and sandpiper-like birds.

Between Charadriidae and Scolopacidae consistent differences can be found in all important skeletal elements. The most prominent features on the caudal side of the proximal humerus and the proximal side of the tarsometatarsus should be enough to illustrate this fact (see Fig. 2).

Charadriidae

Proximal humerus, caudal view:

1. crista pectoralis projecting dorsally, concave insertion area of m. deltoideus maior
2. caput humeri fusing into incisura capitis
3. no marked ligament attachment
4. attachment of m. supracoracoideus situated more proximally

Proximal view of tarsometatarsus:

5. groove for tendon of m. flexor digitorum longus not completely closed
6. groove for tendon of m. flexor hallucis longus situated laterally
7. crista medialis hypotarsi laterally indented by groove for m. flexor p. et pt. dig.2

Scolopacidae

1. crista directed cranially
2. caput bulging ventrally over well marked incisura
3. noticeable ligament attachment
4. attachment situated more distally
5. groove closed to canal
6. groove situated more medially
7. crista more straight, not notched laterally

Some of these differences have already been pointed out by ZUSI & JEHL (1970).

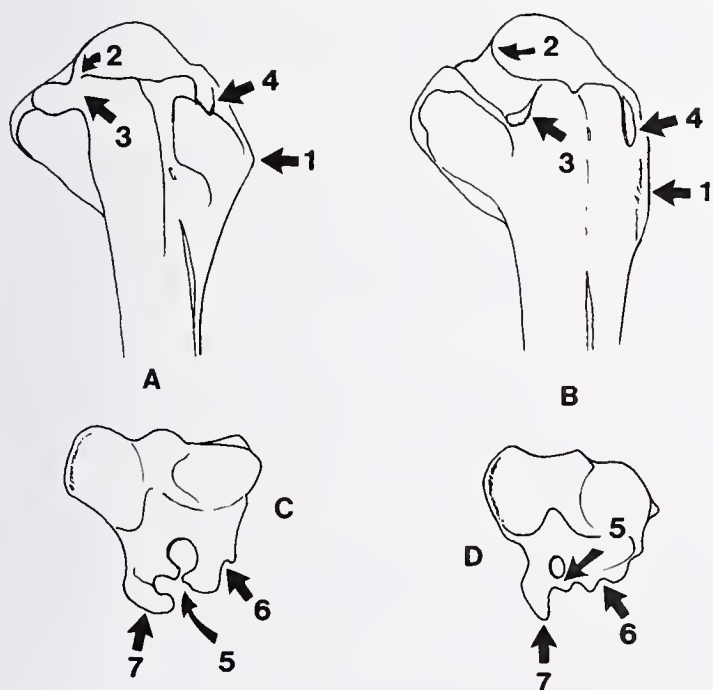


Fig 2: Caudal view of humerus of *Charadrius leschenaultii* (A) and *Scolopax rusticola* (B); proximal view of tarsometatarsus of *Charadrius dubius* (C) and *Mirolia brevirostrata* nov. gen. nov. spec. (D). Not to scale.

For differences between the two families see also BOLZE (1968), who analyzed the histological aspect of the tip of the bill in a number of Charadriiformes. The pits in the tip house Herbst's corpuscles, sensory organs which make the bill a highly sensitive instrument for tactile feeding. His findings support the view that the Scolopacidae are clearly different from the Charadriidae.

Within the Scolopacidae ZUSI (1984) arranges several species on the basis of the morphology of their bills into a morphocline stretching from double rhynchokinesis to strongly developed distal rhynchokinesis: from *Actitis* over *Philomachus* and *Calidris* to *Limnodromus*. The Calidridinae occupy in this cline the middle positions, *Philomachus* being less specialized than *Calidris*.

4. SYSTEMATICS OF THE SUBFAMILY CALIDRIDINAE

Most of the classifications of the Charadriiformes (e.g. KOZLOVA 1961-62; JEHL 1968) recognize a subfamily Calidridinae, the arctic sandpipers. The genera usually placed into this group are *Calidris*, *Eurynorhynchus*, *Limicola*, *Micropalama*, *Philomachus* and *Tryngites*.

Whereas the other genera of Calidridinae are monotypic, *Calidris* itself numbers 18 species, some of which are very closely related.

Some of the older classifications distinguished a greater number of genera (PETERS 1934) and the relationships within the genus *Calidris* seem to be fairly well expressed by the obsolete generic subdivisions. Some recent authors do not concede generic status to *Micropalama* and *Eurynorhynchus*.

Generally, the features used for the many generic subdivisions in older times have become later regarded as adaptive (GLUTZ VON BLOTZHEIM et al. 1975 : 476).

5. GEOGRAPHICAL DISTRIBUTION

The most striking fact about the distribution of the Calidridinae is that their breeding grounds are only found in the Northern Hemisphere and limited there to the high northern latitudes. Most species of *Calidris* breed in the arctic zone, only a few of them reach southwards into temperate regions, so that their main breeding range lies in cold areas north of the 15°C July isotherm (VAN RHIJN 1991). The breeding area of *Calidris alpina* which extends as far south as Britain and the southern Baltic can be considered as uncommon for the genus.

Within the subfamily the breeding range of *Philomachus pugnax* is an outstanding exception, because it reaches as far south as the 23°C July isotherm (VOOUS 1962). In Hungary this breeding area overlaps with that of typical southern species, such as *Glareola pratincola*.

Most of the Calidridinae are long-distance migrants, having their winter quarters in areas far from their breeding grounds. Only a few species, like *C. maritima*, are less migratory. Though some of the species fly as far as to the southern ends of South America, Africa or Australia, the wintering areas tend to be concentrated in the tropics and subtropics of the Northern Hemisphere (USPENSKI 1969).

In terms of classical zoogeography, most Calidridinae inhabit the Palearctic zone or have a circumpolar range. Three species of *Calidris* as well as *Tryngites* and *Micropalama* are limited to the Nearctic.

6. HABITS

The Calidridinae are a group of ground-dwelling wading birds. All of them are strong flyers. During the breeding season most of them occupy various habitats in the Arctic tundra: dry areas in the vicinity of inland water rather than swamps or arctic mountain ranges. They need soft soils and large areas of shallow water. The breeding area of *Philomachus pugnax*, the southernmost species, reaches from the lowlands of the Arctic

through the boreal zone into open habitats of the temperate zone near the ocean and into the steppe of the continental interior.

Outside the breeding season, most sandpipers visit open sandy seashores and estuarine mudflats of temperate to tropical regions, where they are gregarious, often building mixed flocks. Some of them, however, such as *Philomachus* or *Tryngites*, frequent as winter visitors ponds and lakes in the interior and even dry open ground rather than seacoasts. The African winter quarters of *Philomachus* include brackish, saline and alkaline waters. Similar habitats have been mentioned as winter quarters of *Tryngites* in South America.

The food of the Calidridinae consists mainly of invertebrates. By preference they feed during the breeding season on insects and their larvae. They catch molluscs, small crustaceans and worms, and most species also take seeds and other plant material.

They partly locate their food by sight, small animals being picked up from the ground or caught in shallow water. A more typical way of feeding is foraging by touch in somewhat deeper water or extracting prey from superficial layers of soft substrate. Pecking at the surface, as well as jabbing and stitching in shallow mud has been reported. Probing into deeper soft ground is the highest adaptation to tactile feeding reached by Calidridinae.

According to HOERSCHELMANN (1970), who analyzed the functional anatomy of the feeding apparatus of the more common European species, short-billed *Philomachus* is more optically oriented, while longer-billed *Calidris alpina* and *ferruginea* tend to be more tactile. Other species are intermediate in this respect.

7. OSTEOLOGICAL CHARACTERISTICS

As mentioned above it is possible to distinguish Charadriidae and Scolopacidae even on the single skeleton element. Within the Scolopacidae the skeleton is rather uniform, but the shape of the processus supracondylaris on the humerus in the Calidridinae is clearly distinct from other Scolopacidae, the different species of *Calidris* being intermediate between *Philomachus* and *Limicola* (see Fig. 1).

Some further osteological features, which together are typical for the Calidridinae, are shown on Figs. 3 and 4. It is, however, not claimed that they add up to a diagnosis of the subfamily.

The Calidridinae are very close to the Tringinae and to give a differential diagnosis based on postcranial osteological features is not easy. Discussion of the postcranial osteology of the Calidridinae has therefore also to consider closely related taxa like the small-sized and short-legged tringine waders *Actitis* and *Xenus*.

Osteological characters of the head of the Calidridinae are much more conspicuous and were noticed as far back as LOWE (1915), e.g. the short slightly spatulate tip of the bill covered by a great number of small pits.

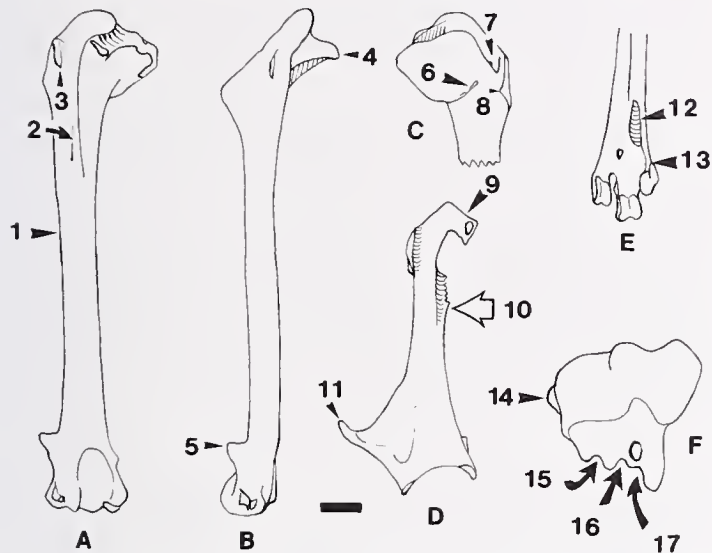


Fig. 3: Several osteological features of the Calidridinae shown on skeleton elements of *Mirolia brevirostrata* nov. gen. nov. spec. Scale 2 mm, F not to scale.

Humerus

A, caudal view: 1) shaft straight, 2) linea m. latissimi dorsi well expressed, 3) impressio m. supracoracoidei situated distally

B, dorsal view: 4) prominent tuberculum ventrale, 5) shape of processus supracondylaris dorsalis

C, cranial view: 6) sulcus n. coracobrachialis cranialis, 7) v-shaped impression for muscle, 8) angulus cristae pectoralis directed cranially

Coracoid

D, cranial view: 9) acrocoracoideum slender, 10) foramen n. supracoracoidei missing, 11) processus lateralis pointed

Tarsometatarsus

E, caudal view: 12) fossa metatarsalis 1 well impressed, 13) trochlea 2 elongated proximally

F, proximal view: 14) attachment of ligamentum collaterale laterale convex, hypotarsus with three grooves (from left to right) for tendons of, 15) m. flexor hallucis longus, 16) m. perforatus dig. 2 and 17) m. perforans et perforatus dig. 2.

Additional characters have been pointed out by KOZLOVA (1961–62) and YUDIN (1965):

– the origin of m. depressor mandibulae leaves an impression on the skull of Calidridinae as opposed to Tringinae.

– in the dorsal bar of the upper jaw of Calidridinae the processus premaxillaria of os nasale are reinforced by the mesethmoid.

These features are explained by the feeding habits of the Calidridinae: 'The structure of the bill and the whole skull of the sandpipers is determined by adaptations to the essential function of the bill: probing, locating and catching of prey in the ground.' KOZLOVA (1961–62: 5).

The same adaptation seems to shape the caudal end of the mandibula (see Fig 4), which also allows distinguishing the Calidridinae from the Tringinae:

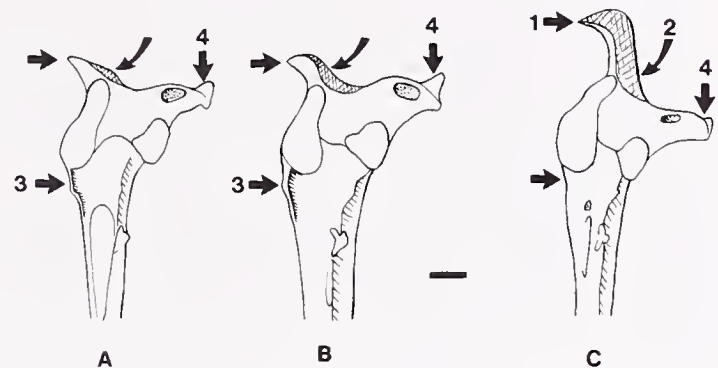


Fig 4: Caudal part of right branch of mandibulae in dorsal view. *Actitis hypoleucos* (A), *Tringa ochropus* (B) and *Calidris alpina* (C). Scale 1 mm.

1) processus retroarticularis longer in Calidridinae than in Tringinae

2) insertion area of m. depressor mandibulae much bigger in Calidridinae

3) insertion of m. adductor mandibulae externus appears as well marked edge in Tringinae.

4) processus medialis slender in Calidridinae, broader in Tringinae

These characters are on the tringine side less pronounced in *Actitis* than in *Tringa*. On the calidridine side *Philomachus* is not as extreme as *Calidris*. Differences between the Calidridinae and *Actitis* are also found on the skull. In *Actitis* it is less compact and its processes are less prominent. The bill is weaker and less spatulate, with a smaller number of pits in the tip.

The fact that *Philomachus* and *Tryngites* are less adapted to tactile feeding is shown by the smaller size and lower number of pits in the tip of their jaws.

Table 1: Number of *foveae corpusculorum nervosorum* in some Calidridinae and Tringinae (* after BOLZE 1968).

Species	number of pits	
	upper jaw	lower jaw
<i>Actitis hypoleucos</i> *	40	50
<i>Xenus cinereus</i>	60	n.d.
<i>Tryngites subruficollis</i>	100	130
<i>Philomachus pugnax</i> *	160	180
<i>Calidris canutus</i> *	155	160
<i>C. minuta</i> *	140	155
<i>C. maritima</i>	180	190
<i>C. alpina</i> *	200	200
<i>C. ferruginea</i>	220	220

The bill of *Eurhynorhynchus* seems to be an adaptation into a different direction of tactile feeding: it shows a large area covered with pits, but is not likely to be used for probing.

Within the genus *Calidris*, number and size of the pits are not only related to body size, but reflect different levels of adaptation to tactile feeding.

8. SIZE AND PROPORTIONS

The smallest members of the genus *Calidris* (*C. minutilla*, *C. temminckii*, *C. minuta* and *C. pusilla*) are about the size of a sparrow and therefore among the smallest Charadriiformes. The biggest species (*C. canutus* and *C. tenuirostris*) reach 25 cm and thus the size of a dove. The size range of *Calidris* overlaps the related genera with the exception of *Philomachus pugnax*, which is noticeably larger (Tab. 2).

The data of Tab. 2 are based on few or even single individuals of each species and can only give a rough idea of size and proportions. Actually there is much overlap

between several species of *Calidris* and some of them, like *C. minuta* and *C. ruficollis* can hardly be separated (GLUTZ VON BLOTZHEIM et al. 1975: 607).

The proportions within the postcranial skeleton are rather uniform throughout the subfamily. A remarkable exception are the long tibiotarsus and tarsometatarsus of *Micropalama*. In *Tryngites* and *Philomachus*, the tarsometatarsus is also relatively long but not as extreme. It reaches in both species almost the size of the humerus, whereas it is clearly shorter in *Calidris*.

Among the little specialized Tringinae, *Actitis* shows a relatively long femur as compared to the average of the Calidridinae. Otherwise the proportions of the postcranial skeleton of *Actitis* and *Xenus* do not differ from the Calidridinae.

Table 2: Measurements on postcranial skeleton elements of Calidridinae and small Tringinae (Length measurements, mm)

Species	Tmt	Tt	Fem	Cor	Hum	Uln	Cmc
Calidridinae							
<i>C. minutilla</i>	19	31.5	16	11.5	23.5	25.5	14.5
<i>C. temminckii</i>	19	32.5	17	12	23.5	25.5	15
<i>C. minuta</i>	20.5	33	16.5	12	23	25.5	14.5
<i>C. pusilla</i>	22	34.5	17.5	12.5	25	26.5	15.5
<i>C. ruficollis</i>	21	34.5	18	13	26	27	15.5
<i>C. mauri</i>	22.5	35.5	18	12.5	25	26	15
<i>Limicola falcinellus</i>	22	37	18.5	14.5	26	27	16
<i>Calidris subminuta</i>	23	36	19.5	12.5	26	28	16
<i>Eurynorhynchus pygmeus</i>	22	35.5	18	14	27	28	17
<i>Calidris alpina</i>	23.5	38	20	14.5	28	29.5	18.5
<i>C. bairdii</i>	23	37	19.5	14	29	31.5	18.5
<i>C. fuscicollis</i>	24.5	41.5	20	14	30	32.5	19
<i>C. alba</i>	26.5	42	22.5	16	30	32	20
<i>Tryngites subruficollis</i>	31	45	25	15.5	32	35	20.5
<i>Calidris melanotos</i>	27	43	24	16.5	32	35	21
<i>C. maritima</i>	25	45.5	24	18	33	35	22
<i>C. ferruginea</i>	30	46	23	16.5	33	35.5	21.5
<i>Micropalama himantopus</i>	42.5	54.5	23	16	34	36.5	22
<i>Calidris pilocnemis</i>	25	45.5	28.5	19	35	36.5	22.5
<i>C. canutus</i>	32	51	28.5	20	40.5	43.5	26.5
<i>Philomachus pugnax</i> , fem.	42				44		
<i>Ph. pugnax</i> , male	52	77	39.5	24	54	60	35
Tringinae							
<i>Actitis hypoleucos</i>	25	41	23.5	15.5	28.5	30.5	18.5
<i>Xenus cinereus</i>	31	48	26	18	35	38	22.5

A much greater diversity is found in the relative length of the bill as compared to the humerus. In the very short-billed species like *Tryngites*, the bill is only about two-thirds of the humerus. The bill of *Philomachus* is also relatively short and does not reach more than about

three-fourths of the length of the humerus. The genus *Calidris* ranges from moderately short-billed species like *C. canutus* and *C. minuta* to long-billed *C. alpina* and *C. ferruginea*, where the bill is 1.5 times the length of the humerus (cf. HOERSCHELMANN 1970).

9. INTRASPECIFIC VARIATION AND SEXUAL DIMORPHISM

The variation of the skeleton within the species of Calidridinae is mainly restricted to differences in size. Greater series of osteological measurements are scarce, but many measurements of wing, bill and tarsus, both on skins and living birds are available (GLUTZ VON

BLOTZHEIM et al. 1975; CRAMP 1983). Measurements of the humerus and wing length of two small species of *Calidris* are shown on Tab 3 and wing measurements of several species of different size have been put together in Tab 4. In addition to the standard deviation, the coefficient of variation has been calculated. It allows comparison of the variation of objects of different size.

Table 3: Variation of length of humerus and wing in two species of *Calidris* (wing measurements from CRAMP 1983).

		length in mm				
		n	range	average	s	v
<i>C. manri</i>			Humerus			
	fem.	17	24.4 – 25.8	25.1	0.44	0.02
	male	13	23.2 – 25.5	24.4	0.54	0.02
	total	30	23.2 – 25.8	24.8	0.62	0.03
			Wing			
	fem.	15	99 – 103	101.0	1.38	0.01
<i>C. minutilla</i>	male	9	94 – 101	97.1	2.38	0.02
			Humerus			
	fem.	12	23.1 – 24.5	23.8	0.45	0.02
	male	12	21.9 – 23.7	23.0	0.56	0.02
	total	24	21.9 – 24.5	23.4	0.65	0.03
			Wing			
	fem.	15	88 – 96	91.6	2.52	0.03
	male	11	86 – 93	89.8	2.10	0.02

Table 4: Measurements of wing, tarsus and bill of several Calidridinae (from GLUTZ VON BLOTZHEIM et al. 1975; CRAMP 1983)

		length in mm				
		n	range	average	s	v
<i>Philomachus pugnax</i>						
Wing	female	855	139 – 175	156.7	3.8	0.02
	male	851	174 – 198	187.6	4.5	0.02
Tarsus	female	31	40 – 46	42.9	1.5	0.04
	male	77	47 – 54	50.2	1.6	0.03
Bill	female	851	26 – 36	30.5	1.2	0.04
	male	535	30 – 39	34.8	1.5	0.04
<i>Tryngites subruficollis</i>						
Wing	female	19	125 – 132	129	2.8	0.01
	male	21	132 – 142	136	2.4	0.02
Tarsus	female	16	28 – 31	29.8	0.9	0.03
	male	14	31 – 34	32.1	1.1	0.03
Bill	female	21	17 – 20	18.5	0.7	0.04
	male	17	19 – 22	20.1	0.8	0.04
<i>Calidris alpina schinzii</i>						
Wing	female	171	109 – 124	117	3.1	0.03
	male	226	105 – 123	112	2.9	0.03
Tarsus	female	169	23 – 28	25.6	0.9	0.04
	male	220	22 – 27	24.1	0.8	0.03
Bill	female	161	27 – 36	31.7	2.1	0.06
	male	218	23 – 36	28.7	1.7	0.06
<i>C. melanotos</i>						
Wing	female	11	126 – 136	131	2.9	0.02
	male	10	139 – 148	144	2.7	0.02
Tarsus	female	23	24 – 28	26.8	1.2	0.05
	male	24	27 – 31	28.9	1.0	0.03
Bill	female	23	26 – 30	27.7	1.3	0.05
	male	24	28 – 32	29.6	1.1	0.04

A coefficient of variation of $v = 0.02$ has been found for the humerus length of males or females of both *Calidris mauri* and *C. minutilla*. Surprisingly enough, the variation of the length of the wing is about the same as that of the humerus. It appears that variation in wing measurements of normally distributed samples, i.e. the males or the females of a given species, is about the same throughout the Calidridinae, regardless of body size. This is the case for the species listed in Tabs 3 and 4. Only the variation of *Calidris alpina schinzii* is slightly greater, possibly because the sample covers a wide geographical range.

For the length of the tarsus the coefficient of variation was found to be between 0.03 and 0.05, thus greater than for the wing. Variation in the length of the bill also exceeds that of the wing. For the species listed in Tab. 4, the coefficient of variation of the bill is about twice that of wing or humerus. These data seem to confirm the observation that differences in the skeleton within the Calidridinae are mainly found in foot and bill.

In the case of fossil material, males and females can usually not be separated and must be considered together. This means that sexual dimorphism must be taken into account and, as can be seen on Tab 5, the sexual size dimorphism can be quite an important factor.

Table 5: Sexual size dimorphism of several Calidridinae (wing measurements from GLUTZ VON BLOTZHEIM et al. 1975; CRAMP 1983). Diff. % = $200 \text{ (male - fem) / (male + fem)}$

		n	length of wing in mm		Diff. %
			range	average	
<i>Philomachus pugnax</i>					
	fem.	855	139 -175	156.7	17.9
	male	518	174 -198	187.6	
<i>Tryngites subruficollis</i>					
	fem.	19	125 -132	129.0	5.3
	male	18	132 -142	136.0	
<i>Calidris melanotos</i>					
	fem.	11	126 -136	131.0	9.5
	male	10	139 -148	144.0	
<i>C. alpina schinzii</i>					
	fem.	171	109 -124	117.0	- 4.4
	male	226	105 -123	112.0	
<i>C. mauri</i>					
	fem.	15	99 – 103	101.0	- 3.9
	male	9	94 -101	97.1	
<i>C. minutilla</i>					
	fem.	15	88 – 96	91.6	- 1.9
	male	11	86 – 93	89.8	
			Length of humerus		
			mm		
<i>C. mauri</i>					
	fem.	17	24.4- 25.8	25.1	- 2.8
	male	13	23.2- 25.5	24.4	
<i>C. minutilla</i>					
	fem.	12	23.1- 24.5	23.8	- 3.4
	male	12	21.9- 23.7	23.0	

In most species of *Calidris* the females are somewhat larger than the males (reversed sexual size dimorphism). In these species the difference in size between males and females is slight. For the humerus length a difference of about 3 – 5 % can be expected.

On the other side in some species, such as *Calidris melanotos* or *Tryngites subruficollis*, the male is noticeably larger. These species show a marked bimodal distribution with differences of up to 10%.

Philomachus shows by far the greatest sexual size dimorphism among the Calidridinae. Judging by the wing measurements of Tab. 5 the humerus of males would almost be 20% longer than in females. This is a quite unusually marked sexual dimorphism within the Calidridinae and has been attributed to the highly derived and maybe terminally evolved mating pattern, the lekking, where fighting between males plays an important role (VAN RHIN 1991).

10. EVOLUTION AND FOSSIL RECORD

The evolution of the Calidridinae during the Pleistocene has been investigated by zoogeographers (e.g. LARSON 1957), but nothing certain is known about the origin and early evolution of *Calidris* and its close relatives. KOZLOVA (1961–62:14) assumed that the Calidridinae might have originated in the middle Neogene.

A relatively recent origin of the subfamily is suggested by its large number of species and the close relationship between most of them. Generally, origin and evolution of the Calidridinae are thought to be closely tied to the tundra, which geologically speaking is a young land-

scape. It is characterised by extreme seasonal changes in temperature and availability of food. In fact, the success in reproduction for the arctic sandpipers seems to depend on exact timing, because adult Diptera and their larvae necessary to feed the young are abundant in the tundra only during a few weeks each summer.

From the Neogene of Europe several fossil species of small scolopacids have been described. Traditionally most of them were placed in the genera "*Totanus*" and *Tringa*. BRODKORB (1967) placed the smaller-sized species into the genus *Erolia* without discussing morphological reasons. Well documented smaller-sized Miocene species are arranged in descending order of size in Tab 6.

Table 6: Fossil species of calidridine size from the Miocene of Europe

Species	Geological age	Neogene Mammal Unit	length of humerus (mm)
<i>Totanus lartetianus</i> M.-E.	Aquitanian	2	47
<i>Totanus majori</i> Lydekker	Tortonian	7 – 8	36 – 37
<i>Erolia gracilis</i> (M.-E.)	Aquitanian	2	32 – 34
<i>Erolia ennouchii</i> Brodkorb	Tortonian	7 – 8	26

The Aquitanian species were found in Langy (France) and described by MILNE-EDWARDS (1867–1871). The Tortonian species were found in La Grive-St.Alban (France) and described by LYDEKKER (1893), ENNOUCHI (1930) and GAILLARD (1939).

Though these species are documented by several entire skeleton elements each, their generic affinities remain unclear. At least for the Aquitanian species it is not likely at all that they belong to the recent genera they have been assigned to. Not even the question whether they belong to the tringine or the calidridine branch can yet be answered with confidence.

A discussion of the relationship of fossil tringine and calidridine birds can only be expected to be more than superficial, if the material includes at least different entire bones of the postcranial skeleton and preferably cranial elements as well. Otherwise any reevaluation and revision of previously described material can only lead to further confusion, as shown by recent publications (e.g. MLÍKOVSKÝ 2002).

Scolopacidae of Pliocene age have been described from North America and Asia. The fossils from North America have been assigned to the extant genera *Tringa*, *Erolia*, *Ereunetes*, *Calidris* and *Micropalama* (BRODKORB 1967). More recently a sandpiper, *Calidris* aff. *melanotos*, from the early Pliocene of Lee Creek, North Carolina, has been described by OLSON & RASMUSSEN (2001).

The Asian fossils are of Pliocene age and have been found in Mongolia and the Baikal region (KUROCHKIN

1985). The small ones have been placed in the extant genera *Tringa* and *Calidris*. Though the assignation of these Pliocene fossils to recent genera is likely to be justified, it should be kept in mind that most of them are poorly documented.

11. SYSTEMATIC PALEONTOLOGY

Order Charadriiformes

Family Scolopacidae

Subfamily Calidridinae

***Mirolia* gen. nov.**

Diagnosis: Calidridine sandpipers of middle Miocene age, ranging in size from smallest recent members of *Calidris* up to *C. alpina*. Bill relatively broad at base and short; dorsal nasal bar only moderately reinforced by mesethmoid; cross-section in middle of dorsal bar broad and flat, against elliptic in *Calidris*; number of foveae corporum nervosorum on tip of upper jaw 80 – 120; upper jaw tip less spatulate than in *Calidris*. Crista tomialis of premaxillare not flattened and without pits. Processus premaxillares of nasalia broad, almost reaching symphysis of bill. Frontal margin of orbita straight, not convex as in *Tryngites*. Processus retroarticularis of mandible shorter than in *Calidris*.

Insertion of m.supracoracoideus on humerus situated less distally than in *Calidris*. Processus supracondylaris dorsalis on humerus more slender than in *Calidris*, *Limicola* or *Eurynorhynchus*. Tarsometatarsus of about the same length as humerus.

Etymology: Contraction of Miocene and *Erolia*.

***Mirolia brevirostrata* spec. nov.** (Figs. 3 and 5)

Holotype: Cranium, 1970 XVIII Steinberg

Type Locality: Steinberg, Nördlinger Ries.

Diagnosis: Type species of genus *Mirolia*, the size of *Calidris mauri*. Impression of m. depressor mandibulae on skull shallow and narrow as in *Philomachus*. Bill short (reconstructed length about 22 mm). Length of humerus: 23.5 – 25.5 mm.

Etymology: From Latin brevis meaning “short” and rostrum “bill” in allusion to its short bill.

Additional material: Praemaxillare, mandibula, coracoid, humerus, ulna, carpometacarpus, femur, tibiotarsus, tarsometatarsus.

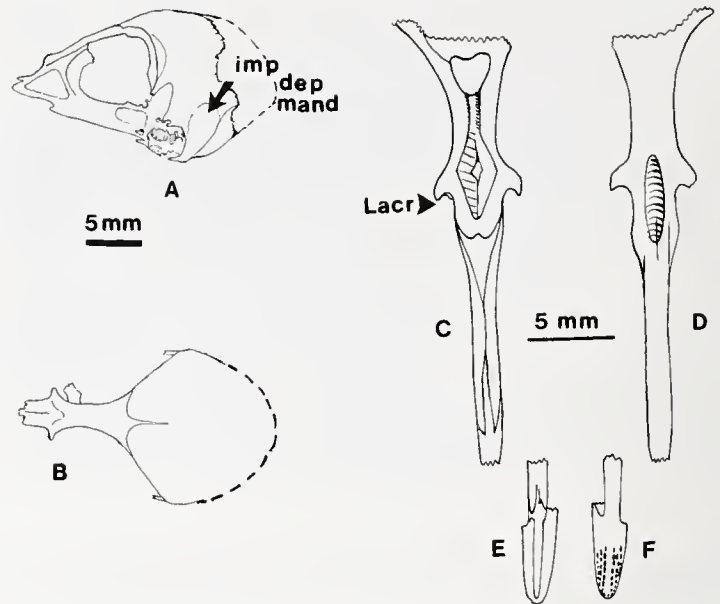


Fig. 5: Cranium (A and B) and bill (C – F) of *Mirolia brevirostrata* nov. spec.

Table 7: Length measurements of *Mirolia brevirostrata* spec. nov. (in mm)

Skeletal element	n	range	average	s	v
Bill (lacrimale to apex)	1	22 (r)			
Coracoid	2	14			
Humerus	9	23.5	24.7	0.6	0.02
Ulna	2	26.5			
Carpometacarpus	10	15.5	16.1	0.5	0.03
Femur	4	18			
Tibiotarsus		34.5			
Tarsometatarsus	2	23.5			

***Mirolia dubia* spec. nov.** (Fig. 6)

Holotype: Left humerus, 1970 XVIII Steinberg

Type Locality: Steinberg, Nördlinger Ries.

Diagnosis: Species of *Mirolia*, the size of *Calidris alpina*. Length of humerus 27 – 28.5 mm, reconstructed length of bill about 26 mm.

Etymology: From Latin dubius = doubtful

Additional material: Praemaxillare, mandibula, coracoid, humerus, ulna, carpometacarpus, femur, tibiotarsus, tarsometatarsus.

***Mirolia parvula* spec. nov.** (Fig. 7)

Holotype: Left humerus, 1970 XVIII Steinberg

Type Locality: Steinberg, Nördlinger Ries.

Diagnosis: In size similar to *C. minutilla*, smallest recent species of *Calidris*. Humerus very slender, crista bicipitalis reaching distally almost as far as crista pectoralis, sulcus nervi coracobrachialis straight.

Etymology: From Latin parvulus = “very small” in allusion to its size.

Additional Material: Coracoid, humerus, carpometacarpus, femur, tarsometatarsus.

***Mirolia ? mascalidris* spec. nov.** (Fig. 8)

Holotype: Mandibula, caudal part of right branch, 1970 XVIII Steinberg mand # 8

Type locality: Steinberg, Nördlinger Ries

Diagnosis: Uncertain species of *Mirolia*, the size of *C. alpina*. Processus retroarticularis less prolonged than in *Calidris* but more than in *Mirolia dubia*.

Etymology: Mascalidris from Spanish más = “more”, meaning more like *Calidris*.

Tentatively referred material: Humerus, tarsometatarsus.

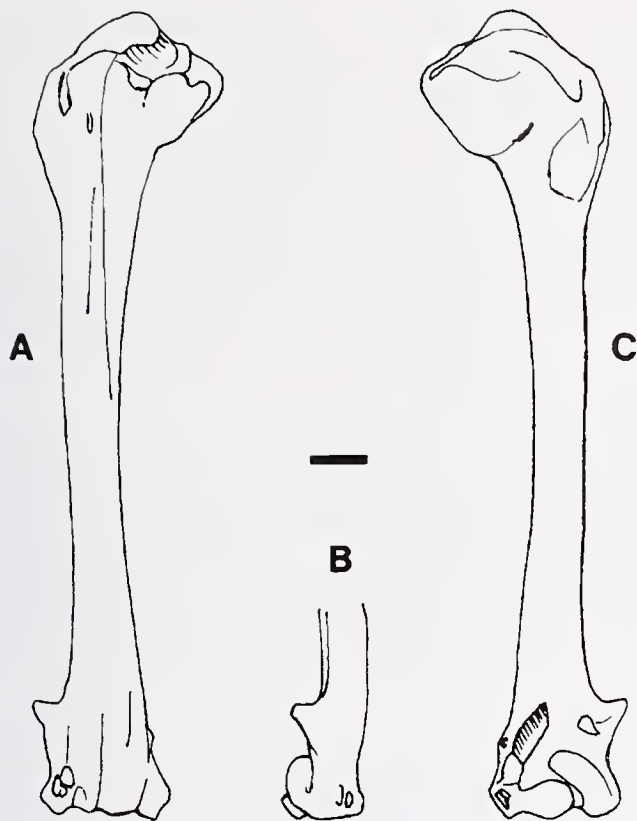


Fig. 6: Left humerus of *Mirolia dubia* nov. spec., caudal (A), dorsal (B) and cranial (C) views. Scale 2 mm.

Feature no. 3 on Fig. 8 distinguishes the mandibula from the Tringinae (*Actitis*, *Tringa*, *Cataprophorus*), while the first and the second feature are similar to *Tryngites*. The process is longer than in *Philomachus* and shorter than in *Calidris* and *Limicola*.

The question whether *M.?* *mascalidris* is congeneric with *Tryngites subruficollis*, can not be decided on the basis of the available fossil material. The fossil is therefore tentatively referred to the genus *Mirolia*.

12. DISCUSSION OF THE RELATIONSHIPS OF *MIROLIA*

The morphological characters of skull and bill of *Mirolia* show that their closest living relatives are the short-billed, more optically oriented Calidridinae *Philomachus* and *Tryngites*.

The more important features shared with these two genera include:

- the shallow and narrow origin of m. depressor mandibulae on the cranium and the corresponding short processus retroarticularis;
- the relatively short bill, with a moderately reinforced dorsal bar.

Table 8: Length measurements of *Mirolia dubia* nov. spec., (in mm)

Skeletal element	n	range	average	s	v
Bill (lacrimale to apex)		26(r)			
Coracoid	2	15.5			
Humerus	5	27 – 28.5	27.7	0.6	0.02
Ulna	4	28.5 – 31			
Carpometacarpus	10	17 – 19	18.4	0.5	0.03
Femur	4	20 – 22			
Tibiotarsus	1	37			
Tarsometatarsus	6	27 – 30	28.2	1.2	0.04

This relationship is further supported by the postcranial features, i.e. the shape of the processus supracondylaris dorsalis on the humerus. In the number of pits in the tip of the upper jaw, *Mirolia brevirostrata* is close to *Tryngites*. *Philomachus*, being of much bigger size, has a greater number of pits. *Calidris* comprises species of gradually differing feeding habits. The relatively short-billed forms, such as *C. canutus* and *C. alba*, are less adapted to tactile feeding than longer-billed *C. alpina* or *C. ferruginea*.

From the close resemblance between the species of *Mirolia* in their osteological features as well as in their proportions it can be deduced that they were more closely related to each other than to any recent species. One of their features in common is the humerus being of

about the same length as the tarsometatarsus. Again, similar proportions are found among recent Calidridinae in *Tryngites* and *Philomachus*, while in the other species the humerus is longer than the tarsometatarsus (see Tab 2), an exception, of course, being *Micropalama limantopus*.

The possibility that *Mirolia brevirostrata* and *M. dubia* are female and male of the same species was discarded. The difference in size is too big. Difference in % such as defined in Tab 5 would be 11.5 for the length of the humerus and 13.3 for the carpometacarpus. This kind of sexual size dimorphism – exceeding that found in *Tryngites* and *Calidris melanotos* – seems unlikely for calidridine birds the size of *Mirolia*.

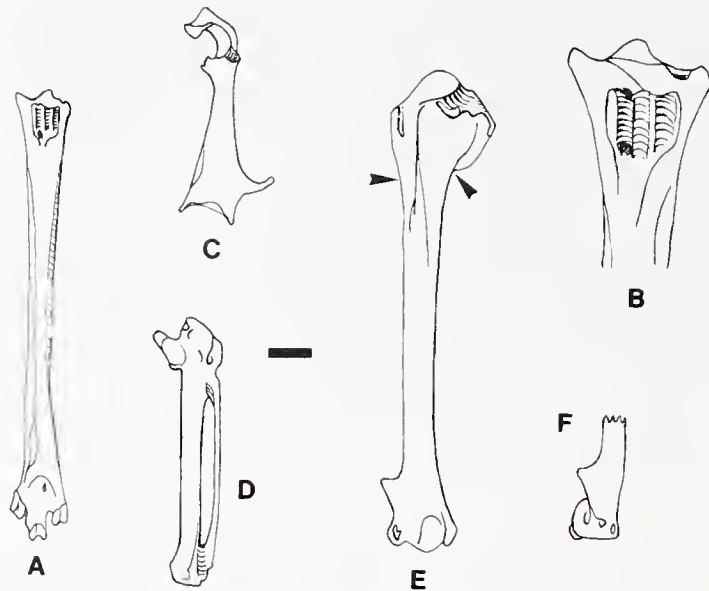


Fig. 7: *Mirolia parvula* spec. nov., right tarsometatarsus caudal view (A), hypotarsus not to scale (B), right coracoid caudal view (C), right carpometacarpus dorsal view (D), left humerus (E) caudal, (F) dorsal view. Scale 2 mm.

Table 9: Measurements of *Mirolia parvula* spec. nov.

Skeletal element	n	length in mm
Coracoid	1	10
Humerus	5	20(r) – 22
Carpometacarpus	4	12 – 14
Femur	2	15 – 17
Tarsometatarsus	2	19 – 20.5

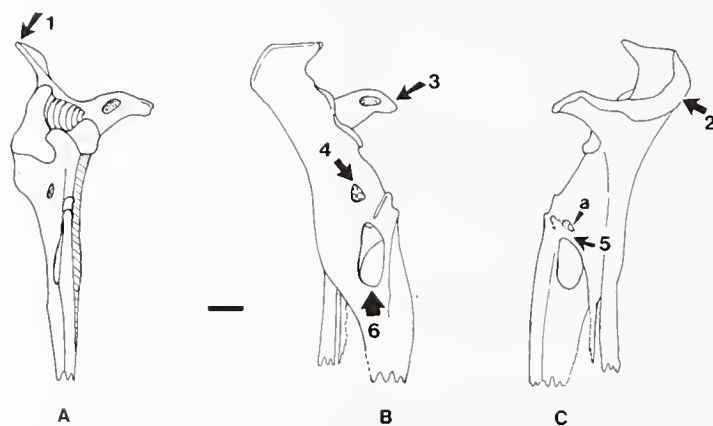


Fig. 8: Caudal part of right branch of mandibula of *Mirolia? mascalidris* spec. nov. in frontal (A), lateral (B) and medial (C) view. Scale 1 mm.

- 1) long processus retroarticularis
- 2) big insertion area for m. depressor mandibulae
- 3) slender processus interior
- 4) foramen pneumaticum
- 5) os complementare joins os suprangulare, thus separating the fontanella from the channel for the n. mandibularis (a)
- 6) open fontanella

13. RESULTS AND CONCLUSIONS

Comparative studies had to be carried out on skeleton material of recent Charadriiformes for the determination of the systematic position of the fossils here described

from the Miocene of the Nördlinger Ries. The osteological data support a separation of the Scolopacidae from the Charadriidae at the family level. This view has already been expressed elsewhere, e.g. in the phylogenetic tree by STRAUCH (1978: fig. 36).

Within the Scolopacidae, osteological differences between Calidridinae and Tringinae are in the first place found on the cranium and the bill. In addition, some complex postcranial structures such as the processus supracondylaris dorsalis of the humerus can help to distinguish the two groups.

The bulk of the fossil remains of small Scolopacidae described here from the middle Miocene of the Nördlinger Ries belongs to several species of *Mirolia*, a new fossil genus within the Calidridinae. Thus the decision of BRODKORB (1967), who assigned a number of fossils from the Miocene to this subfamily is justified.

It appeared that generic determination of Calidridinae of Miocene age can only be based on rather complete fossil material: the diagnosis of *Mirolia* and the more detailed discussion of its systematic position rely in first place on cranial features.

The nearest relatives of the fossil genus *Mirolia* might be the small Scolopacidae of La Grive-St.Alban, especially '*Erolia*' *emouchii*, whose affinities are poorly known.

Though, generally spoken, *Mirolia* seems to have been less adapted to tactile feeding than *Calidris*, it included – as *Calidris* does – species of different degrees of adaptation. The existence of *M.? mascalidris* shows that the morphological level of *Calidris* was almost reached by the middle Miocene, before the spreading of the tundra permitted the expansion and radiation of the arctic sandpipers.

The two monotypic genera *Tryngites* and *Philomachus* still represent in our time the evolutionary level of *Mirolia*. Both may be regarded as relicts of a group, richer in species in the Miocene.

The fossil Calidridinae of the Nördlinger Ries occurred together with birds that are restricted in the present time to the tropics, especially the Ethiopian zone. It could be proven by the presence of an os medullare that the fossil Glareolidae, which definitely are of tropical affinities, did breed at the Ries lake (BALLMANN 1979). Since the recent sandpipers do not breed in the tropics, there is the question whether the fossil Calidridinae did breed at the lake or were migratory birds breeding further north and visiting the Ries in the non-breeding season. Though the material includes several subadult individuals, there is no conclusive evidence that *Mirolia* actually was nesting near the lake. The possibility of migration is made likely by the close morphological relationship to

recent Calidridinae, which are all migratory. If so, nothing much can be said about the breeding areas of the species of *Mirolia*. Climate in the middle Miocene of Europe was still very mild. Glaciation does not seem to have appeared in the Arctic before the Pliocene and therefore the tundra landscape would not have existed yet in big scale. However, an environment suitable for the breeding of calidridine birds may already have existed in the highlands of northern Europe.

If the fossil Calidridinae were migrants, they cannot add much to our knowledge of the paleoclimate of the Nördlinger Ries. The habitat required by *Mirolia* in the non-breeding season would likely be open ground and shallow water with muddy shores. This kind of habitat has already been postulated by BOLTEN (1977) for the molluscs described by him from the Ries lake. A moderate salinity of the lake is quite compatible with the occurrence of the Calidridinae described.

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